

Evolutionary Ecology Research, 2007, **9**: 41–50

The relative contribution of individual and kin selection to the evolution of density-dependent dispersal rates

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ABSTRACT

Questions: What are the relative contributions of kin selection and individual selection to the evolution of dispersal rates in fragmented landscapes? How do environmental parameters influence the relative contributions of both evolutionary forces?

Features of the model: Individual-based simulation model of a metapopulation. Logistic local growth dynamics and density-dependent dispersal. An optional shuffling algorithm allows the continuous destruction of any genetic structure in the metapopulation.

Ranges of key variables: Depending on dispersal mortality (0.05–0.4) and the strength of environmental fluctuations, mean dispersal probability varied between 0.05 and 0.5.

Conclusions: For local population sizes of 100 individuals, kin selection alone could account for dispersal probabilities of up to 0.1. It may result in a ten-fold increase of optimal dispersal rates compared with those predicted on the basis of individual selection alone. Such a substantial contribution of kin selection to dispersal is restricted to cases where the overall dispersal probabilities are small (<0.1). In the latter case, as much as 30% of the total fitness of dispersing individuals could arise from the increased reproduction of kin left in the natal patch.

Keywords: dispersal rate, evolutionary modelling, individual-based model, kin competition, metapopulation.

INTRODUCTION

Dispersal is a key process for the survival of populations living in heterogeneous or fragmented landscapes. It influences the spatial and temporal distribution of local population sizes as well as population extinction (Lande *et al.*, 1999; Kean and Barlow, 2000; Kendall *et al.*, 2000; Hanski, 2001; Poethke and Hovestadt, 2002), and the genetic structure of metapopulations (Levins, 1969; Hastings and Harrison, 1994; Olivieri *et al.*, 1995; Pannell and Charlesworth, 2000). On the other hand, local extinction, population size, and the genetic structure in a metapopulation are the major determinants of evolutionarily stable (ES) dispersal rates (Ronce and Olivieri, 1997; Travis *et al.*, 1999;

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Ronce *et al.*, 2000a, 2000b; Heino and Hanski, 2001; Parvinen *et al.*, 2003; Poethke *et al.*, 2003). Consequently, an inherent evolutionary interaction exists between all these factors.

Since the early papers of Gadgil (1971), van Valen (1971), and Hamilton and May (1977), the complex interaction between genetic and demographic factors on the one hand and dispersal on the other hand has stimulated a multitude of theoretical and empirical studies on the evolution of dispersal strategies. Most theoretical models are based on rather general considerations of the trade-off between the costs and benefits of dispersal using one of two major modelling approaches. One set of studies has focused on the reduction of kin competition as a driver for the evolution of dispersal. The authors of these studies were mainly interested in the genetic structure of populations (e.g. Hamilton and May, 1977; Comins *et al.*, 1980; Frank, 1986; Irwin and Taylor, 2000). Another set of studies has considered the role of individual selection (e.g. van Valen, 1971; Levin *et al.*, 1984; McPeck and Holt, 1992; Metz and Gyllenberg, 2001). In the latter models, the benefit for a dispersing individual lies in the possibility to leave more offspring when arriving in a habitat patch with better conditions for reproduction – that is, an empty or at least less densely populated patch, or a patch of better habitat quality.

Clearly, in natural systems the evolution of dispersal is simultaneously driven by both individual and kin selection. Unfortunately, few attempts have been made to combine these two principal approaches into a single model and to compare the relative contribution of individual and kin selection to the evolution of dispersal. Consequently, it is difficult to decide on the validity of the predictions based on the different approaches and to estimate the relative error incurred by the exclusive use of one or the other. The analytic model of Gandon and Michalakis (1999, 2001) focuses on the effect of kin competition and inbreeding but also covers the influence of externally driven local extinction on ES-dispersal rates. Their model is well suited to study the effect of direct (offspring number) and indirect (reproductive success of kin) fitness benefits in the evolution of dispersal. However, it does not foresee the evolution of density-dependent dispersal strategies and is based on rather restricted assumptions about the dynamics as well as the genetics of a metapopulation.

In individual-based models of the evolution of dispersal, kin competition emerges by default. The model of Travis and Dytham (1998, 1999; Travis *et al.*, 1999) thus implicitly covers both individual and kin selection. However, their model does not allow the separation of the influence of the two aspects and they did not distinguish between the relative contribution of each of these mechanisms to the evolution of dispersal rates.

In an individual-based simulation model based on a marginal value approach, we previously reported that dispersing individuals had consistently fewer offspring than philopatric individuals (Poethke and Hovestadt, 2002). We assume that this discrepancy is compensated by the added benefit transferred to remaining kin in the case an individual leaves its natal patch. Recently, Bach *et al.* (2006) presented a simulation model that allows reduction of the influence of kin competition on the evolution of dispersal by decoupling reproduction and competition in the simulated life-cycle. They found a pronounced influence of kin selection on dispersal at low dispersal cost and relatively high dispersal rates only. However, their model only allows for the exclusion of the effects of direct sib competition, not of higher-order kin effects. Such higher-order effects will be particularly important when overall dispersal rates are low and a strong genetic structure emerges. In this paper, we present the results of simulation experiments where the genetic structure of the metapopulation is either left intact or systematically homogenized by the random redistribution of individuals between habitat patches. The random redistribution of individuals before dispersal does not influence direct fitness gains of dispersal but eliminates any kin-related benefits. The

comparison of both types of simulation experiments allows quantification of the relative contribution of direct and indirect fitness to the selection of ES-dispersal rates for different environmental conditions and for species with different population dynamics.

THE MODEL

Our simulation experiments are based on an individual-based model of insect dispersal in patchy landscapes of n_{patch} habitat patches, all with the same capacity K (see below). We simulate a population of sexually reproducing organisms. Thus, each individual has a gender, is affiliated with a specific patch i , and carries two alleles at a diploid locus. The alleles determine the density dependence (p_c) of the individual's dispersal probability d (see below). Alleles are inherited from the mother and a father randomly selected among the males of the same patch. The values for these alleles may change by mutation. As we had no prior knowledge of the complexity of the fitness landscape in our problem, we based the mutation algorithm on the idea of simulated annealing (Martin-Mayor, 2005; Michalewicz, 2005) and let mutation rates decline exponentially over time [$m(t) = 0.1 \exp(-2.5t/t_{\text{max}})$; with the maximum number of generations $t_{\text{max}} = 10,000$ (see also Poethke and Hovestadt 2002)]. Individuals disperse simultaneously before mating and reproduction. Regardless of patch origin, dispersing individuals die with probability μ during transition.

Local population dynamics are governed by density-dependent reproduction of individuals. After mating with a local male, a female gives birth to Λ offspring, where Λ is a Poisson-distributed number with a patch- and time-specific mean $\Lambda_{\text{mean}}(t, \text{patch})$. For each time step, we draw a value for $\Lambda_{\text{mean}}(t, \text{patch})$ from a log-normal distribution with mean λ and standard deviation σ , the latter determining the degree of environmental fluctuations. We assume environmental fluctuations to be uncorrelated in space and time. Offspring develop into mature individuals with density-dependent survival probability s (cf. Hassell, 1976):

$$s = \frac{1}{(1 + aN_i)^\beta} \quad (1)$$

where $a = (\lambda^{1/\beta} - 1)/K$, N_i = population size in patch i , K = carrying capacity of patch i , and β = density dependence.

After maturation, offspring disperse with probability d . This probability is determined by the actual population density $C_i (= N_i/K)$ and an individual's genetic constitution. We assume that dispersal probability is sensitive to local population density according to the non-linear model developed by Poethke and Hovestadt (2002), simplified for equal patch capacity:

$$d = \begin{cases} 0 & \text{if } C_i \leq p_c \\ 1 - p_c/C_i & \text{if } C_i > p_c \end{cases} \quad (2)$$

For each individual, the value of p_c is the mean value of the individual's two corresponding alleles. We have previously demonstrated that the mode of dispersal (e.g. nearest-neighbour dispersal or global dispersal) has only very small quantitative effects on evolving dispersal probabilities (Poethke and Hovestadt, 2002; for similar conclusions, see Comins *et al.*, 1980; Gandon and Rousset, 1999; Gandon and Michalakis, 2001). We thus assume global dispersal throughout this paper.

In addition to this ‘standard’ model, we ran a modified version (‘shuffled’) of our simulation program. In this version, we prevent the emergence of a genetic substructure by shuffling the whole metapopulation in each generation. After all individuals reach maturity but before dispersal, the number of individuals in each patch is recorded. Subsequently, all individuals from all patches are collected and randomly redistributed among patches with the constraint that the previous population size of each patch is maintained.

In all simulation experiments, the metapopulation consisted of $n_{\text{patch}} = 100$ local populations of carrying capacity $K = 100$ individuals. We performed experiments with different values for the mean rate of population increase ($\lambda = 2, 4, 6$), density dependence ($\beta = 0.5, 1.0$), dispersal mortality ($\mu = 0.05, 0.1, 0.2, 0.4$), and environmental stochasticity ($\sigma = 0.0, 0.5, 1.0, 2.0$). To control for the influence of initial trait composition on the evolving dispersal probability, we initialized five replicate simulation experiments with different initial dispersal tendencies ($p_C = 0.6, 0.8, 1.0, 1.2, 1.4$) for each parameter combination. This gives a total of $(2 \times 3 \times 4 \times 4 \times 5 = 480)$ simulation experiments for both the standard as well as the shuffled scenario. At the start of each experiment, the populations were initialized with K individuals. Sex was randomly attributed to individuals.

RESULTS

Direct fitness of dispersing and philopatric individuals

Depending on dispersal mortality (μ) and the strength of environmental fluctuations (σ), the ES-dispersal probabilities after 10,000 generations scatter widely between values close to 0 and values near 0.6 (for details, see Poethke and Hovestadt, 2002; Poethke *et al.*, 2003). The initial value for the threshold density p_C has no influence on the simulation results. We can thus be sure that p_C has reached its evolutionarily stable value in all experiments. In some scenarios with extremely small emerging dispersal rates ($m < 0.01$), the complete metapopulation went extinct. We excluded such simulations from further analysis.

The direct fitness of dispersing and philopatric individuals can be derived from a detailed record of population size ($N(i, t)$), the number of offspring ($\Phi(i, t)$), and the number of emigrants ($E(i, t)$) for each patch (i) and every generation (t) (see Appendix). At equilibrium, the mean number of offspring per individual ($F_{\text{individual}}$) should equal 1.0 whatever the parameter combination. However, as some individuals die during dispersal, surviving individuals get slightly more offspring ($F_{\text{individual}} > 1$; Fig. 1) and their reproductive output must necessarily increase with dispersal mortality (μ) and dispersal probability (m): $F_{\text{individual}} = (1 - \mu \cdot m)^{-1}$. The mean number of offspring for dispersing individuals is influenced by their survival probability ($1 - \mu$) and will decrease almost linearly with dispersal mortality: $F_{\text{emigrant}} = F_{\text{individual}} \cdot (1 - \mu)$ (Fig. 1).

Based on individual selection arguments only, individuals should only leave a patch when the expected number of offspring when dispersing (F_{emigrant}) is at least equal to the number of offspring they would have had if they had stayed in their natal patch ($F_{\text{sacrifice}}$). Consequently, marginal value theory predicts that in evolutionary equilibrium the potential number of offspring an emigrant sacrifices in its natal patch should equal its expected number of offspring when leaving ($F_{\text{sacrifice}} = F_{\text{emigrant}}$) (Metz and Gyllenberg, 2001; Poethke and Hovestadt, 2002; Roff, 2002; see also Doncaster, 2000). However, our simulations show that this is only the case in the shuffled scenario (Fig. 1b). As long as the genetic structure of the population is not

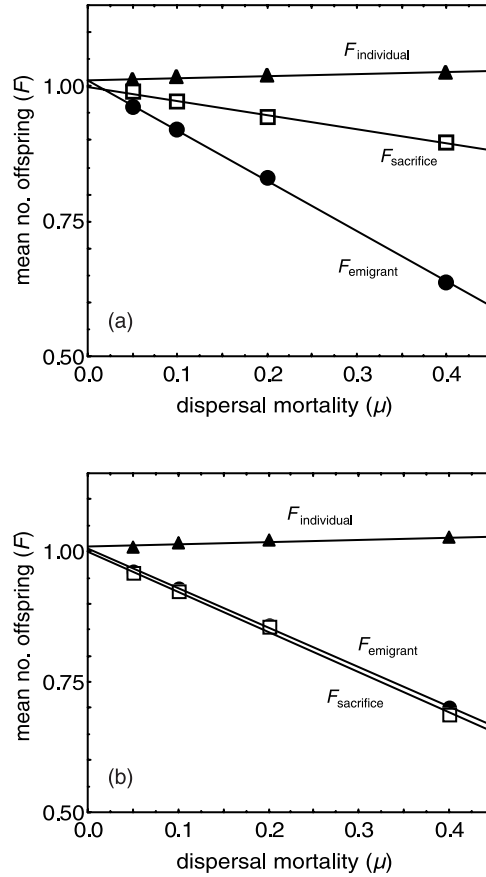


Fig. 1. (a) Mean number of offspring (direct fitness) for all individuals ($F_{\text{individual}}$), for dispersing individuals (F_{emigrant}), and the expected number of offspring for a dispersing individual if it had stayed ($F_{\text{sacrifice}}$) as a function of dispersal mortality (μ). Results of 480 simulation experiments with the standard model (unshuffled). Parameter values: $\sigma = 0.0, 0.5, 1.0, 2.0$; $\lambda = 2, 4, 6$; $\beta = 0.5, 1.0$; initial values of $p_C = 0.6, 0.8, 1.0, 1.2, 1.4$. Standard deviations for mean values were always < 0.05 and are not shown for clarity. For definition of F , see Appendix. (b) Same as (a) but for results from the shuffled scenario. Standard deviations for mean values were always < 0.05 and are not shown for clarity.

continuously destroyed, dispersers always leave less offspring than philopatric individuals (Fig. 1a). In fact, the difference in offspring number increases markedly with increasing dispersal mortality (μ). Increasing dispersal rates will necessarily result in a declining genetic difference between local populations and the influence of kin competition should consequently be most pronounced in the case of low inter-patch dispersal. We have previously shown that evolutionarily stable dispersal probability decreases with increasing dispersal mortality (μ) (Poethke and Hovestadt, 2002). Consequently, the increase in the difference between the direct fitness of dispersing and philopatric individuals with increasing dispersal mortality (μ) is readily explained by the increasing influence of kin selection at low overall dispersal probabilities.

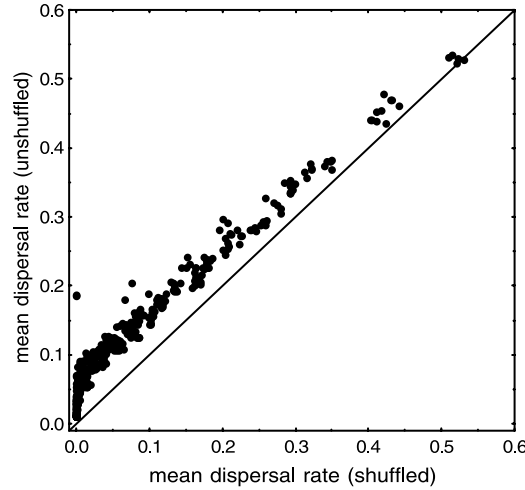


Fig. 2. Comparison of ES-dispersal probabilities between standard simulations (unshuffled) and simulations without genetic substructure of the metapopulation (shuffled). Results of ($2 \times 480 =$) 960 simulation experiments. Parameter values: $\sigma = 0.0, 0.5, 1.0, 2.0$; $\lambda = 2, 4, 6$; $\beta = 0.5, 1.0$; $\mu = 0.05, 0.1, 0.2, 0.4$; initial values of $p_c = 0.6, 0.8, 1.0, 1.2, 1.4$.

The relative contribution of kin selection

In comparison, we find consistently higher emigration probabilities in the standard versus the shuffled scenario (Fig. 2). The difference between the two scenarios strongly depends on the evolved mean dispersal probability, which is mostly determined by the strength of environmental fluctuations (σ) and dispersal mortality (μ) [for a detailed analysis of the factors that determine dispersal probabilities, see Poethke and Hovestadt (2002) and Poethke *et al.* (2003)]. For high dispersal mortality (μ), dispersal probabilities may fall below 0.01 in the shuffled scenario. For the same model parameters, the dispersal probability in the standard scenario will surpass 0.10. Thus, the influence of kin selection may result in a ten-fold increase in dispersal rates if dispersal probability is low. However, at sufficiently high dispersal probabilities, the increase in dispersal tendency caused by kin competition almost vanishes (Fig. 2). As a genetic substructure in the metapopulation does not emerge if many individuals disperse successfully, this result is in complete agreement with our expectations.

DISCUSSION

For a broad range of growth (λ, β) and environmental (σ, μ) parameters, we compared the evolution of density-dependent dispersal in a case that allows for the emergence of a genetic structure with a case that prevents it. In all our standard experiments (no shuffling), dispersing individuals had consistently fewer offspring than philopatric individuals. Since differences in direct fitness between dispersing and philopatric individuals vanished when individuals were redistributed between patches before reproduction (shuffling), we conclude that our shuffling approach successfully suppressed any influence of kin selection on the evolution of dispersal.

While the influence of individual selection on ES-dispersal rates is determined by

inter-patch differences in population density and dispersal mortality (Poethke and Hovestadt, 2002), kin selection is driven by genetic differences between local populations (Taylor, 1988; Gandon and Michalakis, 2001; Perrin and Goudet, 2001). In particular for small dispersal rates, we find a very pronounced genetic substructure in our metapopulations ($F_{ST} > 0.3$). In this case, the relative contribution of indirect fitness gains could be substantial [for the relation between F_{ST} and the coefficient of relatedness in local populations, see Perrin and Goudet (2001)], and there will be a significant difference in evolved dispersal rates between experiments in the ‘shuffled’ and in the ‘unshuffled’ scenario.

Nevertheless, if we want to derive estimates of the relative influence of kin selection on dispersal rates in a particular situation, we have to keep in mind that the genetic structure of a metapopulation is not solely determined by dispersal: dispersal reduces genetic differences between local populations, but genetic drift enhances inter-patch differences. Thus, any mechanisms that increase genetic drift (e.g. a decrease in local population size or increased population fluctuations) will result in greater genetic distances between local populations and consequently in an increase in kin competition.

Our simulations take into account density dependence, local population dynamics, genetic structure, and environmental heterogeneity as well as the *interdependence* between these variables and ES-dispersal probabilities. Any model that allows for the simultaneous impact of kin and individual selection allows us in principle to analyse the relative influence of both processes for the evolution of dispersal. However, some of these models ignore density dependence and consider only *externally* caused extinction as the driving force behind individual selection (e.g. Comins *et al.*, 1980; Gandon and Michalakis, 2001). Such restrictions make it very difficult to evaluate the interdependence between these factors and to produce quantitative estimates of the relative strength of both individual and kin selection in the evolution of dispersal strategies.

By decoupling reproduction and competition, Bach *et al.* (2006) eliminated the effect of direct sib competition in their model but not of competition between more distantly related relatives. In contrast to our findings, they concluded that sib competition plays only a moderate role in the evolution of dispersal and that its influence is restricted to situations where dispersal costs are low and dispersal rates are high. However, due to their approach they underestimate the influence of overall kin competition, particularly at low dispersal rates where genetic drift will lead to a pronounced genetic structure of the metapopulation. Consequently, we trace the difference between their conclusion and ours to the fact they did not take account of higher-order kin competition.

In a model based on pure kin selection, Gandon and Rousset (1999) found that – in contrast to our claim in ‘The model’ section – the mode of dispersal (nearest-neighbour dispersal or global dispersal) will have a pronounced effect on evolving dispersal rates *if* costs of dispersal are low. This contradicts the findings of Poethke *et al.* (2003) and Bach *et al.* (2006), who found no significant influence of the mode of dispersal on dispersal probabilities for low dispersal cost. However, our simulations make clear that at low cost of dispersal the genetic distance between local populations will be low, as individual selection favours high rates of dispersal. Consequently, in such a situation individual selection dominates the evolution of dispersal, kin selection plays a negligible role, and the mode of dispersal can be ignored.

In true metapopulations [i.e. systems characterized by significant population turnover and low rates of (successful) dispersal (Levins, 1969; Hanski and Simberloff, 1997)], kin competition is likely to be the more important factor defining the level of emigration observed. In

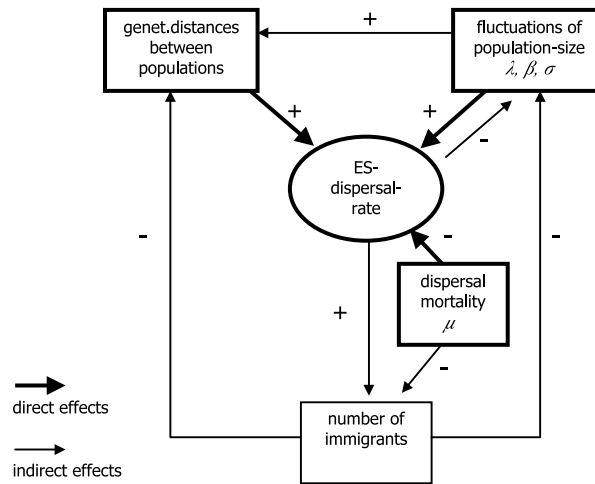


Fig. 3. Schematic representation of the regulation of ES-dispersal probabilities. Dispersal is directly influenced by genetic differences between populations (+), fluctuations of population size (+), and dispersal mortality (-). On the other hand, dispersal reduces both the genetic structure of the metapopulation and inter-patch fluctuations in population size. The latter effect is caused by immigration and, particularly in the case of density-dependent dispersal, emigration from crowded patches.

agreement with other studies based on a pure ‘kin approach’ (e.g. Plantegenest and Kindlmann, 1999), our simulations suggest that even at very high costs of dispersal considerable dispersal probabilities may evolve. As the interactions between population dynamics, the genetic structure of the metapopulation, and ES-dispersal rate are fairly complex (Fig. 3), it is rather promising that, at least for logistic growth of local populations (as has been used in our simulations), the observed increase in ES-dispersal probability due to kin selection is so tightly correlated with dispersal probability across all the scenarios we have investigated.

ACKNOWLEDGEMENTS

This work was supported by the DFG (grant #PO-244/3-1) and the European Commission (Mac-Man Project, grant #EVK2-CT-2001-00126). We thank Peter Chesson and Calvin Dytham for their valuable comments on an earlier draft of the manuscript.

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APPENDIX

We calculate direct fitness of dispersing and philopatric individuals from population size ($N(i, t)$), the number of offspring ($\Phi(i, t)$), and the number of emigrants ($E(i, t)$) for each patch (i) and every generation (t). Mean number of offspring per individual ($F_{\text{individual}}(t)$) is:

$$F_{\text{individual}}(t) = \frac{1}{N_{\text{total}}(t)} \sum_{i=1}^{n_{\text{patch}}} \Phi(i, t) \quad (\text{A1})$$

Emigrants are randomly assigned to a new patch (global dispersal). Thus successful dispersers on average get patch mean number of offspring

$$F_{\text{patch}}(t) = \frac{1}{n_{\text{patch}}} \sum_{i=1}^{n_{\text{patch}}} \left[\frac{\Phi(i, t)}{N(i, t)} \right] \quad (\text{A2})$$

However, dispersers experience dispersal mortality (μ). Thus, only a fraction of dispersers will reach a new patch. Consequently, the expected number of offspring for an emigrant ($F_{\text{emigrant}}(t)$) is:

$$F_{\text{emigrant}}(t) = (1 - \mu) \cdot F_{\text{patch}}(t) \quad (\text{A3})$$

Dispersing individuals do not reproduce in their natal patch, but in the patch they reach after dispersal. Thus, they sacrifice potential offspring at home for expected offspring in their target patch. If an emigrant had not emigrated but stayed in its natal patch, it would have had the same number of offspring as the philopatric individuals in this patch. Thus, the mean number of offspring sacrificed by a disperser is:

$$F_{\text{sacrifice}}(t) = \frac{1}{E_{\text{total}}(t)} \sum_{i=1}^{n_{\text{patch}}} E(i, t) F(i, t) \quad (\text{A4})$$

We registered offspring number ($F(t)$) every 50 years. To reduce the influence of random demographic fluctuations, we calculated mean values for the last $n_{\text{gen}} = 100$ values taken over the last 5000 generations of each simulation experiment.